The ecological impact of dumping massive amounts of *Sargassum* in beach and forest ecosystems

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**Abstract**

Anthropogenic activities and urbanization have increased the frequency and scale of seaweed strandings (pelagic *Sargassum*) along Caribbean and West African shores. Such strandings present significant ecological and economic challenges. To mitigate these impacts, people remove substantial amounts of *Sargassum* biomass from coastlines and dump it into nearby ecosystems. We investigated the ecological implications of *Sargassum* deposition using manipulative field experiments whereby realistic amounts of Sargassum (several cubic meters) were added to beach and forest ecosystems. Contrary to expectations based on ecological theory (i.e., the Home Field Advantage hypothesis), our findings reveal comparable decomposition rates between beach and forest ecosystems. Additionally, a "litter bag" experiment revealed that decomposition processes differed between ecosystems - microbes dominated decomposition in the forest and a combination of microbes and talitrid amphipods drove decomposition on the beach. Sargassum additions increased nitrate levels to agricultural levels in both habitats, though these levels peaked later in the beach than the forest. This influx stimulated plant growth in the beach but not the forest. Although the beach initially contained low plant cover (5%), *Sargassum* additions dramatically increased cover of invasive Bermuda grass, *Cynodon dactylon*, to >75%. This effect on Bermuda grass spilled over to adjacent areas of the beach beyond the initial plot footprints. Thus, the bottom-up effect of *Sargassum* addition to plant fertilization overwhelmed toxicity effects of additional salts or chemicals associated with seaweeds. Sargassum additions more strongly impacted beach arthropods, with an increase in talitrid amphipods, spiderss, ants, and flies. Crawling arthropods in pitfall traps consisted of arachnids and hymenopterans, mainly spiders and ants at both sites, and talitrid amphipods at the beach (Fig. 7). Our findings challenge the notion that naïve ecosystems are incapable of processing novel subsidies. These habitat-specific impacts should be considered when making decisions about where and how to dump massive amounts of Sargassum into adjacent terrestrial habitats.

*Keywords: Algae blooms, Home field Advantage, Sargassum, Spatial subsidies*

**Introduction**

Human population growth and urbanization deliver high levels of nutrients into coastal waters that stimulate algal blooms (Teichberg et al. 2010). Such blooms present economic and ecological challenges to impacted countries (Lapointe 1997, Teichberg et al. 2010, Smetacek and Zingone 2013, Rodríguez-Martínez et al. 2023). Seasonal or periodic landings of macroalgae typically confer benefits to beaches by serving as a foundation for and contributing to the fertilization of coastal dunes and serve as a resource subsidy to food webs (Polis et al. 1997, Huxel and McCann 1998, Anderson and Polis 1998, Marczak et al. 2007, Yang et al. 2010, Spiller et al. 2010, Williams and Feagin 2010, Wright et al. 2013, Piovia-Scott et al. 2013). However, massive blooms disrupt ecological processes and can be a nuisance to coastal communities. For example, macroalgal blooms can clog fishing nets, impede the passage of boats, and release unpleasant or harmful chemicals (Teichberg et al. 2010, Smetacek and Zingone 2013, Resiere et al. 2021, Rodríguez-Martínez et al. 2023). Also, beach-cast macroalgal blooms can create anoxic conditions and shade benthic taxa (Hauxwell et al. 2001, Teichberg et al. 2010, Van Tussenbroek et al. 2017, Rodríguez-Martínez et al. 2019).

Because seaweed blooms negatively impact coastal economies and environments, it is common for this biomass to be removed from shorelines and dumped into adjacent habitats. However, the impacts of dumping massive quantities in adjacent habitats remain unknown. There is a need for manipulative experiments to understand how such anthropogenic activities subsidize and influence communities in recipient habitats.

Currently, residual biomass from hydrocolloid extractions (e.g., agar, alginate, and carrageenan) and removal of seaweed blooms contributes a significant amount of waste that is discarded in landfills and natural terrestrial habitats (Dang et al. 2023). There is only a nascent understanding of the impacts of seaweed dumping on these terrestrial habitats. However, such impacts could be likely for at least two reasons. First, macroalgae added to terrestrial habitats are known to improve soil fertility (Pereira et al. 2019). Indeed, the direct application of macroalgae as an agricultural fertilizer is a traditional practice in places like Patagonia, Argentina, that receive large amounts of seaweed wrack (Eyras et al. 2008, Gibilisco et al. 2020, Madejón et al. 2022). Second, seaweeds may negatively impact recipient terrestrial habitats because of the addition of salts, toxins (e.g., heavy metals), and material that otherwise could be difficult to decompose. Further, the lack of co-evolution of terrestrial organisms in recipient habitats with seaweed impairs our ability to predict the impacts of seaweed dumping on land.

An important bloom-forming seaweed that increasingly impacts coastal economies and ecology and habitats where it is dumped is the pelagic seaweed *Sargassum* that consists of a mixture of *S. fluitans* and *S. natans* (Gower et al. 2013, Rodríguez-Martínez et al. 2020, Chávez et al. 2020). Although floating *Sargassum* patches have been observed in the tropical and subtropical Atlantic Ocean since the 1800s (Brooks et al. 2018, Uribe-Martínez et al. 2022), massive strandings of *Sargassum* are a relatively new phenomenon. For example, since 2011, the shores of Caribbean countries, West Africa, and the Gulf of Mexico are often smothered in *Sargassum* deposits that are regularly over 1m deep (Doyle et al. 2015) and can cover the entire length and breadth of beaches (as pictured in Chávez et al. 2020). The extent of beached *Sargassum* can be impressive - the northern sector of the Mexican Caribbean is now estimated to receive volumes ranging from 10,000 - 40,000 m³ of *Sargassum* per kilometer of beach per year with most landings happening between April and September (Rodríguez-Martínez et al., 2023). Furthermore, *Sargassum* bloom intensity and frequency is predicted to continue to increase (Smetacek and Zingone 2013, Rodríguez-Martínez et al. 2023).

This recent influx of *Sargassum* deposition on beaches negatively impacts coastal economies and ecologies. *Sargassum* degrades pristine white sand beaches and turquoise waters that attract tourists to the Caribbean. Such tourism provides the basis for the majority of the Gross Domestic Product for many of these countries. For example, the Mexican state of Quintana Roo attracted nearly 15 million tourists and generated an income of approximately US$10.8 billion in 2021 even with high *Sargassum* deposition (Rodríguez-Martínez et al., 2023). As a result, increasing *Sargassum* deposition presents a significant obstacle for the entire region.

In addition to the economic impacts, there are negative ecological consequences of leaving *Sargassum* on beaches. Without removal of *Sargassum*, leachates and organic matter reduce oxygen and pH levels, and increase turbidity, sulfur, and ammonia concentrations (Van Tussenbroek et al. 2017, Chávez et al. 2020, Rodríguez-Martínez et al. 2023). For instance, a significant *Sargassum* beaching event in 2018 was associated with a coastal fish and invertebrate mortality event, where hypoxic conditions led to the demise of 78 species of neritic fish, crustaceans, echinoderms, mollusks, and polychaetes (Van Tussenbroek et al. 2017, Rodríguez-Martínez et al. 2019).

To minimize the negative impacts of beached *Sargassum*, humans deploy barriers offshore to catch *Sargassum* with various success and remove *Sargassum* from beaches. All strategies require that the collected biomass be moved into adjacent habitats including beach dunes, forests, quarries, farms, and garbage dumps (R. DeSantiago, R. Rodriguez-Martinez, J. Long, pers. obs.) Unfortunately, the impacts of this large-scale “experiment” are largely uncertain for at least two reasons. First, the capacity of local communities that have historically received smaller amounts of *Sargassum* (e.g., beach dune communities) to keep pace, decompose and incorporate this material is unlikely given the sheer volume of material needing processing. Second, *Sargassum* is being dumped into some habitats that are completely naïve to seaweed subsidies and might lack the capacity to decompose and utilize this material (e.g., forests).

Ecological theory suggests that local adaptation through coevolution would result in faster decomposition of litter by familiar or experienced soil communities, termed ‘*the home field advantage’* (Bocock et al. 1960, Gholz et al. 2000, Pugnaire et al. 2023). Thus, beach-cast *Sargassum* should decompose more quickly over sand dunes than forest soil. Furthermore, terrestrial predator foraging in beach-cast macroalgae is a common feature in coastal ecosystems (Kirkman and Kendrick 1997, Rose and Polis 1998, Dugan et al. 2003, Colombini and Chelazzi 2003, Kenny et al. 2017), but less is known about the responses of terrestrial insects that are likely some of the first responders to such detrital inputs. Moreover, previous work with *Sargassum* biomass showed a fertilization effect on plants on shorelines Bahamian islands (Piovia-Scott et al. 2013) and there have been efforts to use *Sargassum* as a fertilizer for vascular plants. Yet, the fertilization effect of *Sargassum* in forest has not been tested.

Here, we used manipulative experiments to examine the ecological consequences of dumping large amounts (i.e., several cubic meters) of *Sargassum* in habitats currently used as *Sargassum* dumps (i.e., beaches and forests). At both habitats, we created realistic piles of *Sargassum* with paired, unmanipulated controls, and surveyed plots quarterly for one year. We estimated pile decomposition by estimating pile volume and by measuring mass change of smaller amounts of *Sargassum* in mesh bags with different accessibility to microbes and arthropods. We surveyed soil respiration and soil ammonium, nitrate, and dissolved organic carbon. To study *Sargassum* impacts on the plant community, we surveyed vegetation on plots and adjacent to plots. To measure the impact of *Sargassum* on the arthropod community, we used pitfall traps and sticky traps to survey crawling and flying arthropods, respectively.

**Methods**

Between July 23, 2022, and August 3, 2022 (hereafter, August 2022), we created *Sargassum* (~4 m3) piles in a beach and forest habitat in Puerto Morelos, Quintana Roo, Mexico. These habitats are commonly targeted as dumping sites and this region has been greatly impacted by increased deposition of *Sargassum* onto beaches since 2011. All experiments were permitted by the Mexican government (CNANP-00-007) and the local property managers (Moon Palace Resort and Dr. Alfredo Barrera Marín Botanical Garden, for the beach and forest habitat, respectively). Both sites provide limited access to the public and therefore, should be minimally impacted by human disturbance. This region experiences a “hot subhumid climate with rainfall during the summer”, “a mean annual temperature of 27oC”, and “a mean annual precipitation of 1,105 mm” (Garcia 1973, Sánchez Sánchez and Islebe 1999).

Because people dump *Sargassum* high on beaches and in beach dunes, our beach manipulation was deployed at the transition from the beach dune to the beach (20.99343° N, -86.82442° W). The beaches in this region are formed from calcareous sand derived from coral reefs and shells, as well as limestone from the Yucatan Peninsula (Castillo and Moreno-Casasola 1996, Mendoza-González et al. 2016). This coast is inhabited by >200 plant species that are mostly salt-tolerant, low, non-woody plants (<30 cm high) belonging to cosmopolitan families (e.g., *Poacea*, *Astracea*, and *Leguiminosae*). Additionally, woody species occur at higher elevations (Islebe et al. 2015). *Ambrosia hispida, Tournefortia gnaphalodes, Suriana maritima, Tribulus cistoides, Ipomoea pes-caprae, Sesuvium portulacastrum, Sporobolus virginicus, Canavalia rosea, Okenia hypogea, Croton punctatus Tribulus cistoides, Ernodea littoralis, Scaevola plumierii, Coccoloba uvifera Pithecellobium keyense*, *Cakile lanceolata, Erithalis fruticosa,* and *Ernodea litteralis,* are widely distributed in this area (Castillo and Moreno-Casasola 1996, Mendoza-González et al. 2016)*.* Further, we identified African Bermuda grass (*Cynodon nlemfuensis,* hereafter “grass”) throughout the site.

Because people dump *Sargassum* in forest clearings that allow access for large dump trucks, our forest manipulation was deployed on the perimeter of a forest clearing in a botanical garden (Jardín Botánico ECOSUR “Dr. Alfredo Barrera Marín”; 20.84400° N, 86.90278° W). This forest is 4.2 km away from known forest *Sargassum* dumps. The dry forests in this region are considered tropical semi-evergreen forests (Miranda and Hernández-X. 1963) that reach canopy heights of 15-20 m (Sánchez Sánchez and Islebe 1999). Characteristic trees in the forest include *Brosimum alicastrum*, *Talisia olivaeformis*, *Manilkara zapota*, *Myrcianthes fragrans*, and *Dideroxylon gaumeriq*. Characteristic understory species include *Drypetes lateriflora*, *Coccoloba diversifolio*, *Gymnanthes lucida*, *Thrinax radiata*, and *Coccothrinax readii* (Sánchez Sánchez and Islebe 1999). The forest soil type is Lithosol-Rendzina and thus has a well-developed topsoil, no subsoil, and is shallow (<30cm) over limestone (Islebe et al. 2015).

Our manipulation crossed Habitat (Beach, Forest) with *Sargassum* (Addition, Control). At each site, we haphazardly selected locations for paired plots (separated by 9 m between pile centers) and then randomly assigned one plot of each pair to either *Sargassum* addition or unmanipulated control (n=5). For *Sargassum a*ddition plots, we created large piles of *Sargassum* (~1.88 m radius) with a backhoe or wheelbarrows (for the beach and forest habitat, respectively). *Sargassum* piles were initially larger at the beach than the forest (5.25 ± 0.03 and 3.31 ± 0.09 m3, beach and forest, respectively; two-sample t test, t = 5.3058, df = 4.5363, p-value < 0.05). These pile sizes are within the range that humans currently dump in beaches and forests in this region (pers. obs.). All *Sargassum* used in this experiment was collected from drift *Sargassum* accumulated in the ocean at the offshore barriers installed by Moon Palace Environmental Services. As a result, terrestrial organisms (e.g., talitrid amphipods) should have initially been absent from the experimental *Sargassum*. Beach plots were placed parallel to the water line.

To consider seasonal variation and successional patterns in the impacts of *Sargassum* dumping, we surveyed plots at deployment (August 2022 and three additional dates: November 2022, March 2023, and August 2023). During each sampling period, we assessed pile decomposition and the impact of these manipulations on edaphic conditions, soil respiration, plants, and arthropods. To sample the same locations within plots across sampling dates, we marked the plot center with a flag, and we placed a rope circle around this flag whose radius was the mean radius of *Sargassum* addition plots at the initial deployment date (radius = 1.88m). We confirmed the position of the center flag using multiple photographs of each plot before placing the rope circle.

To estimate decomposition of entire *Sargassum* piles, we measured pile volume at each time point. Pile volume was determined with the equation of an elliptic cone (*V=1/3 πabh)*, where a=length of the semi-major axis of the pile footprint, b=the length of the semi-minor axis perpendicular to a, and h=pile height. Because pile volume is confounded by water loss and we wanted to understand the relative contribution of microbes and macrofauna to decomposition, we also measured decomposition of smaller amounts of *Sargassum* (wet mass = 235 ± 0.4g) deployed in each habitat inside bags with small and large mesh openings (0.18 mm and 10 mm; n=10). Decomposition in small mesh bags should have been driven by microbes since these bags excluded larger arthropods, whereas decomposition in large mesh bags was the result of both microbes and mesodetritivores smaller than 10mm.

Mesh bags deployed in the beach habitat were placed adjacent to the large pile manipulation. Mesh bags deployed in the forest habitat were placed in a nearby forested location (20.8636° N, -86.9138° W) from August-November 2022, because this mesh bag experiment was started prior to identification of a forest site for deployment of the large pile manipulation. However, all forest mesh bags were moved to the botanical garden adjacent to the large pile manipulation in November 2022. At each sampling date (i.e., November 2022 and March 2023), we measured *Sargassum* wet mass. At the final sampling in March 2023, we also dried *Sargassum* to directly measure final dry biomass. We estimated starting dry biomass by calculating a dry:wet mass ratio and multiplying starting wet biomass by this ratio. These measurements were then used to calculate decomposition as a percentage of the initial dry biomass.

In addition to the mesh bags providing a more accurate assessment of decomposition, the large mesh bags also provided the opportunity to quantify the invertebrates attracted to *Sargassum*. After initial deployment of mesh bags in August 2022, we collected them after 7 days, removed all arthropods, and weighed and returned the *Sargassum* biomass into the mesh bags before returning them to the sites. After 3 months, we collected all bags and repeated these steps. Arthropods found in large mesh bags were identified to order and counted. Unfortunately, due to vandalism, we were unable to recover the large mesh bags from the beach habitat in March 2023. Thus, at this point we obtained final wet and dry mass and concluded the mesh bag experiment.

To understand if *Sargassum* additions increased soil nutrients, we collected 50 mL sediment cores from all plots. To minimize disturbance to the *Sargassum* piles, sediment cores were collected ~30 cm towards the plot center from plot edges. We cleared overlaying *Sargassum* and leaf litter before collecting soil. Samples from August 2022, March and August 2023 were dried using the lowest setting of a conventional oven (3 hrs, 190⁰C) then kept at -80⁰C until transported to San Diego State University (SDSU) in August 2023 where they were kept at -20⁰C until analysis. Because we did not have access to an oven in November 2022, these samples were dried at SDSU in a 65⁰C oven for 6 hr before the analysis in December 2023. To assess the accumulation of  ammonium and nitrate in sediment, we conducted a Spectrophotometric Nitrate assay using the methods outlined in Pérez Castro et al. (2020) adapted to our sample sizes (10 g). We assessed the dissolved organic carbon content of sediment samples using the method outlined in Bartlett and Ross (1988).

To determine the impact of *Sargassum* additions on soil respiration, we used two separate techniques. First, we collected gas samples that were later analyzed for CO2 levels with Mass Spectroscopy. Gas samples were collected from inverted containers (1.87 L) placed ~30 cm towards the plot center from plot edges. Prior to pushing these containers into the sediment, we removed overlying detritus. Gas was collected from containers with vacutainers immediately after deployment and then one hour later. The samples were analyzed by gas chromatography with flame ionization at San Diego State University.

*Plant Community Impacts*

To assess the effect of *Sargassum* on plant cover directly on plots (i.e., plot interior), we surveyed percent cover using 0.5 x 0.5 m quadrats with a 100-point grid. In August and November 2022, we haphazardly tossed a marker over the shoulder onto the interior and placed a quadrat where the marker landed (n=3). In March and August 2023, we switched to random sampling (by randomly selected cardinal directions and distances from the plot center). For all plant surveys, we only recorded the top “canopy” layer of plants beneath the 100 points (supplementary Fig. 3, 4).

*Plot perimeter survey*

To assess the effect of *Sargassum* on plant cover beyond piles, we surveyed percent cover adjacent to the edge of the initial plot footprint of all treatments in August 2022 and 2023. We placed a quadrat at the edge of *Sargassum* plots and an equivalent location on control plots (i.e., 1.88m from the plot center), at four opposing poles or points of tangency. We measured percent cover using the methods described in the section above. For two of these poles, we also surveyed plant cover at two additional distances extending away from the pile edge [D1 and D2 = 0.75 and 1.5 m at both sites (August 2022); 0.52 and 1.27m at beach and 0.62 and 1.37m at forest (November 2022); 0.32 and 1.07m at beach and 0.43 and 1.18m at forest (March 2023); supplementary Fig. 2]. Distances varied between dates and habitats because quadrats were placed 0.75 and 1.5m from the edge of the *Sargassum* piles and then an equivalent distance was used for control plots. After the fact, we corrected these two distances at each date and habitat because we were interested in understanding how far away from the initial plot footprint any *Sargassum* effect would appear. We recognize this approach limits our ability to rigorously compare across habitats. In March 2023, we did not see variation between sampling distances and decided to drop this portion of the survey in the interest of sampling efforts and time (see results section).

Additionally, because in March 2023 Bermuda grass was so prevalent at the beach sites and there were no obvious patterns observed in forest grasses or with other specific plant taxa in either habitat, we collapsed all plants other than Bermuda grass into one category in the Forest, and both sites in August 2023. Thus, we present “grass” and “other plants” for all sampling periods in the figures. Furthermore, by November 2022 the *Sargassum* treatments had already decreased in volume and footprint area, which meant that quadrats placed on the edge of *Sargassum* for the perimeter survey had been moving over sampling periods, thus in August 2023 we decided to sample at 1.88m from the centers of *Sargassum* piles in the same way we sampled control plots. Because the quadrats on the “perimeter” were actually sampling over the original footprint of *Sargassum* plots, we excluded them from analysis and figures, as they do not accurately represent edge effects.

*Arthropod Community Impacts*

To assess the effect of *Sargassum* on the crawling arthropod community, we placed yellow plastic cups (210 ml) at two opposing poles of each plot for 24 hours. Pitfall traps were buried flush with the substrate and filled approximately halfway with water and ~5 drops of dish soap to break the surface tension and prevent arthropods from escaping. Because we wanted to assess arthropod abundance at the same time for each habitat to reduce variability from deployment dates, we waited until all *Sargassum* piles were completed at the beach before installing pitfall and sticky traps. At the point of installation, two *Sargassum* piles had been complete for two days, two had been completed for one day, and the traps were deployed after the final pile was made. All *Sargassum* piles were completed in one day in the forest and arthropod traps were deployed on the same day. After 24 hours, we collected the entire contents of each trap, and then counted and identified arthropods to order.

To assess the effect of *Sargassum* on the flying arthropod community, we placed two double-sided sticky cards (127mm x 76mm, Catchmaster ®), attached to wire rods, on each plot. The sticky traps were placed ~130mm above the substrate or *Sargassum* piles, ~1m from the center of the plot. After 24 hours, we photographed all sticky traps *in-situ* to process at a later time. Arthropods were counted on both sides of sticky traps and identified to order. We note that such traps could also catch non-flying amphipods (e.g., talitrid amphipods that often move via jumping).

**Statistical Analyses**

To test decomposition of *Sargassum* piles, we analyzed pile volume as a percent of starting volume using a Linear Mixed Effects Model (LMEM), with site and sampling trip as the main effects and their interaction. We included *Sargassum* pile number in the model as a random factor to account for differences in starting volume. To test if decomposition of *Sargassum* differed in mesh bags with and without arthropod access, we used a LMEM with treatment, habitat, sampling trip as the main effects and their interactions, and bag identification number as a random factor to account for repeated measures. To test if arthropod abundance in large mesh bags differed between sites over time, we used a Linear Model with arthropod order, habitat, and sampling trip as main effects with their interactions. To test the effects of *Sargassum* addition on edaphic conditions we conducted three linear models with ammonium, nitrate, or DOC as a response variable with treatment as the main effect, habitat and sampling trip as interacting factors.

To test the effect of *Sargassum* additions on plant cover on the interior and the perimeter of plots, we directly compared percent cover of grass and “other plants,” in *Sargassum* addition plots to paired controls by habitat at each sampling period. We used *Cohen’s d*, which quantifies the difference in means between two groups (i.e., control vs. addition), divided by the weighted average of the standard deviations between both groups to determine the effect size. Using this standardized effect size allows for comparisons of magnitude of the effect between groups on a common scale (i.e., small d≈0.2, medium d≈0.5, and large d≈0.8 effect sizes). We analyzed the effect sizes of *Sargassum* addition on crawling and flying arthropod abundances using the same method.

All statistical analyses and visualizations were conducted using the R Programming Language (R Core Team, 2023). Linear models and LMEM were conducted using the R base and ‘nlme’ packages. Necessary assumptions were met for statistical analyses and post-hoc tests were conducted as needed.

**Results**

Dumped *Sargassum* decomposed in both habitats, as measured both via change in pile volume (Supplementary Fig. 1) and biomass loss in the mesh-bag experiment (Fig. 1). The majority of decomposition occurred during the first four months. After one year, pile volume decreased by >85%. Pile volume as a percent of starting volume differed between habitats in November 2022 (LMEM: Estimate = 2.020, Std. Error = 4.857, t-value 3.918, p <0.001), but this effect was not observed in later sampling periods (p=0.65).

In November 2022, habitat interacted with mesh size to influence decomposition of *Sargassum* in mesh bags (LMEM: Estimate = 21.05, Std. Error = 5.973, t-value 3.525, p <0.001). At this time point, decomposition in the forest was similar for large and small mesh bags suggesting that microbes drove decomposition in the forest. In contrast, decomposition in the small mesh bags at the beach was only 51% of the decomposition in the large mesh bags, suggesting that detritivores between 0.18-10mm played a much more significant role at the beach. Decomposition in large mesh bags between habitats did not differ suggesting similar total decomposition in both habitats (Estimate = 8.78, Std. Error = 4.18, p = 0.43). Consistent with the pile volume temporal pattern, most decomposition occurred in the first four months of the mesh-bag experiment (LMEM: Estimate -17.805, Std. Error = 6.352, t-value = -2.803, p < 0.005). Unfortunately, we lost the large mesh bags at the beach in March.

In August 2022, habitat interacted with sampling trip to influence total count of arthropods in large mesh bags (LM: Estimate = 27.68, Std. Error = 8.63, t-value = 3.198, p = 0.001). Fewer arthropods were attracted to these large mesh bags in the forest (Estimate = -28.50, Std. Error = 6.12, t-value = -4.66, p < 0.001), likely due to high abundances of talitrid amphipods caught at the beach. In contrast, no amphipods were found in the mesh bags during November sampling at either habitat.

*Soil nutrients*

Ammonium levels were consistently higher in forest soils where they peaked in August and November 2022 (Fig. 3A, B). Although there was no treatment effect on ammonium levels from *Sargassum* addition in either habitat (LM: Estimate =0.738, Std. Error = 3.889, t-value = 0.19, p=0.85), there was a trend for *Sargassum* additions to suppress ammonium in forest soils in November 2022. *Sargassum* addition increased nitrate levels in both habitats (LM: Estimate =55.887, Std. Error =12.61, t-value = 4.432, p < 0.001). Nitrate levels peaked later in the beach than in the forest (March 2023 and November 2022, respectively; Fig. 3C, D). *Sargassum* addition significantly increased DOC at both locations (LM: Estimate =199.32, Std. Error = 56.93, t-value = 3.501, p < 0.001; Fig. 3E, F).

*Soil respiration*

*Sargassum* addition tended to increase carbon dioxide production in November 2022 (Fig. 4). However, neither the treatment effect, site effect, or their interaction were statistically significant (ANOVA: F(1,12)=1.679, p=0.219; F(1,12)==0.953, p=0.348, and F(1,12)==0.025, p=0.878; respectively).

*Plant community impacts*

Although the beach initially contained low plant cover (5%, supplementary Fig. 3, 5), *Sargassum* additions dramatically increased grass cover to >75% (Fig. 5A, C; 2 sample t-test: -9.861, df = 18.057, p<0.001). This effect began to appear in November 2022 but was most apparent in March and August 2023. In contrast, grass cover remained low in control plots throughout the year (<10%; Fig. 5A). Non-grass plants only displayed weak responses to *Sargassum* additions. Although the effect was weaker than directly in the plots, the effect of *Sargassum* additions at the beach spilled over to increase grass cover 3.8x just beyond the plot perimeters (after one year *d*=1.02, Fig. 6A, C). There was no effect beyond perimeter in November 2022 or March 2023, so we did not continue to survey at distances beyond the perimeter (November 2022 and March 2023, *d*=0). This spillover effect was taxon-specific as *Sargassum* additions at the beach did not strongly impact non-grass plants outside of the plots in November 2022, March 2023, or August 2023 ( *d=*0.45, 0.2, 0.16, respectively).

Similar to the beach, the forest floor contained low plant cover at deployment (4%; supplementary Fig. 4, 6). Unlike the beach, *Sargassum* additions in the forest did not increase plant cover for any taxon within plots (Fig. 5B, D). There was a slight increase in effect size in “other plants” in the forest habitat in March 2023 (*d*=0.09, Fig. 5D), but this was the result of a plot that was covered by a *Cucumis* plant that was not rooted within the *Sargassum* pile. After removing this plot from the analysis, the effect size was large and negative, indicating percent cover of “other plants” was much higher in control plots compared to *Sargassum* pile interior (*d*=-1.18). Although there was not a direct effect of *Sargassum* additions on forest plots, there was a spillover effect – *Sargassum* additions increased non-grass plants at plot perimeters (*d*=0.56 Fig. 6B, D).

*Arthropod community impacts*

Crawling arthropods in pitfall traps consisted of arachnids and hymenopterans, mainly spiders and ants at both sites, and talitrid amphipods at the beach (Fig. 7). Adding *Sargassum* at the beach immediately increased amphipod abundance 42x in August 2022 (Fig. 7A, C, E). After the initial sampling of plots in August 2022, amphipods were rare [only 1 amphipod was found in a control plot in November 2022 and 1 in a *Sargassum* plot in March 2023 (Fig. 7C,E)]. Additionally, *Sargassum* additions at the beach initially increased arachnids and hymenopterans (August 2022). This effect remained for hymenopterans during later sampling events but not arachnids (Fig. 7A, C, E). In the forest, *Sargassum* addition only weakly affected crawling arthropods (Fig. 7B, D, F). Importantly, no amphipods were found in forest pitfall traps during any of the sampling periods (Fig. 7 B, D).

Flying arthropods sampled on sticky traps at the beach consisted of dipterans and hymenopterans, mostly flies and wasps (Fig. 8). On the initial deployment of the experiment, amphipods (21 ± 7) were also captured on sticky traps, presumably because they move via jumping. Beach *Sargassum* additions initially increased dipterans 23x more than controls– however, this effect diminished over time (Fig. 8A, C, E). *Sargassum* additions also increased hymenopteran abundance – but this effect was not apparent until November and March. Similar to the beach, *Sargassum* additions to the forest increased both dipterans and hymenopterans (Fig. 8B, D, F). However, the dipteran effect in the forest was stronger and delayed.

**Discussion**

Realistic amounts of *Sargassum* (i.e., several cubic meter piles) dumped into adjacent terrestrial habitats commonly used as dumping grounds (e.g., beach dunes and forests) decomposed at similar rates. Most decomposition of *Sargassum* occurred within the first four months (August 2022 - November 2022). Interestingly, the drivers of decomposition differed between habitats - microbes predominantly drove decomposition in the forest, while talitrid amphipods played an equivalent role as microbes on the beach. Decomposing *Sargassum* also increased soil nitrates and dissolved organic carbon, with nitrates entering the soil several months earlier in the forest. Additionally, there was a trend for *Sargassum* dumps to increase soil respiration beneath the piles. While *Sargassum* dumping modified edaphic conditions in both habitats, the aboveground plant and arthropod communities were more strongly impacted at the beach. *Sargassum* additions at the beach dramatically increased the cover of the invasive Bermuda grass to over 85% total coverage, and attracted talitrid amphipods, flies, wasps, and ants. Conversely, in the forest, Sargassum additions had a weaker or neutral effect on plants and arthropods.

Although *Sargassum* decomposed at similar rates in the two habitats, the roles of microbes and mesodetritivores were habitat-specific in at least two ways. First, decomposition by microbes was twice as fast in the forest. This finding contrasts with the Home Field Advantage hypothesis that predicts that microbial use of subsidies should be faster in the experienced habitat (i.e., the beach). Despite the naivete of forest microbes to seaweed detritus, the more favorable abiotic conditions (e.g., increased humidity and reduced temperature) and ambient microbial communities may have overwhelmed the evolutionary co-occurrence of forest microbes and seaweed detritus. Second, mesodetritivores contributed to approximately half of overall decomposition in the beach but were relatively unimportant in the forest. Beach mesodetritivores were dominated by talitrid amphipods, a detritivore that specializes in seaweed wrack that colonized our *Sargassum* piles within days (Wildish et al. 2016).

Habitat-specific roles of microbes and mesodetritivores could influence how *Sargassum* subsidies move through food webs and habitats where it is dumped. When *Sargassum* is dumped into forests, the dominance of microbes as decomposers suggests that this material will be incorporated into subterranean food webs in soils directly beneath the piles and perhaps diluted into local water tables. In contrast, the material from *Sargassum* dumped into beaches will more quickly enter aboveground food webs, including those away from the piles because talitrid amphipods that feed on this material are mobile and are consumed by a variety of terrestrial predators including birds and lizards (Dugan et al. 2003, Wright et al. 2020).

Although *Sargassum* dumping increased soil nitrate levels in both habitats, it only stimulated plant production in the beach habitat. *Sargassum* plots at the beach were quickly colonized by the invasive Bermuda grass within eight months. This colonization was associated with an increase in total vegetation cover from 5 to 85%. The lack of a fertilization effect in the forest could be related to at least four factors. First, forest soils may not have been nutrient limited at the start of the experiment. In support of this hypothesis, we observed higher ammonium, nitrate, and dissolved organic carbon in forest soils than beach sediments. Second, another abiotic factor may have limited productivity in the forest. For example, forest plots beneath the tree canopy may have been primarily limited by light. Third, the timing of the nutrient pulse may have differed from the phenology of forest plants relative to beach plants. Fourth, forest plants may have been dispersal-limited. In this regard, it was interesting that the only forest *Sargassum* plot to stimulate plant productivity was colonized by cucumber with vine growth.

The positive impact on plants suggests that any potential toxic or negative effects from the addition of *Sargassum* seaweeds were outweighed by the fertilization effect. This strong fertilization potential by *Sargassum* has been seen in previous studies (Piovia-Scott et al. 2013, Adderley et al. 2023). Local farmers and entrepreneurial companies interested in converting *Sargassum* biomass to marketable fertilizers have long recognized the potential for *Sargassum* to fertilize terrestrial habitats. We found that nitrate levels following the addition of *Sargassum* were comparable to agricultural levels and similar to those in pot experiments using *Sargassum* as a biofertilizer (i.e., >100 mg Nitrate per kg soil; Adderley et al. 2023), indicating an increase in soil fertility. Additionally, our unpublished data revealed that arsenic levels after one year were orders of magnitude lower than the concentration necessary to be toxic to Bermuda grass (Weaver et al. 1984). While these findings are promising, it is important to acknowledge certain caveats. Our study did not rigorously assess the contents of arsenic in plant tissues or if leachates from *Sargassum* decomposition enter belowground waterways. Thus, understanding the accumulation of arsenic up the food web is crucial in order to fully assess potential negative impacts on consumers.

The arthropod response to *Sargassum* was habitat-specific and appeared to be a direct response to *Sargassum* and not Bermuda grass. On the beach, amphipods, flies, and ants initially showed a strong response, which was likely due to the moist environment and scent of fresh wrack. This effect, however, diminished over time. Because the location of the piles at the beach were above the high tide line, it was interesting that amphipods traversed the entire length of the beach to access the freshly deposited *Sargassum*. The lack of amphipods on subsequent trips was perhaps related to the lower palatability of dried *Sargassum* or alternately, easier access to fresh wrack deposits on the shoreline. Conversely, ants continued to utilize the wrack piles throughout the experiment, possibly due to the physical structure of *Sargassum* piles providing shelter from the environment. Spiders also responded initially, possibly due to their predatory nature and a response to amphipod densities, but this effect diminished in later sampling periods. Wasps showed a delayed but strong response after four months in both habitats, suggesting that this response was not due to an attraction to plants. However, it remains unclear if the numerical response of wasps was a predatory reaction to increased flies, especially in the forest habitat.

Decisions about dumping *Sargassum* will depend on management priorities. For example, if the goals are to minimize impact on aboveground communities including invasive grasses or to minimize impact on beach tourism, our study would suggest continuing to prioritize dumping in forests. However, it is important to note that although arsenic was not found to be toxic to Bermuda grass, it did leach from the *Sargassum* into the soil. This raises concerns about the possibility of arsenic entering groundwater, particularly in areas like the Yucatan Peninsula where the water table is shallow and underneath karst, which could have implications for human health (Rodríguez-Martínez et al. 2020, Vázquez-Delfín et al. 2021). Beaches are unlikely to process massive amounts of *Sargassum* and leaving that biomass on the beach could fuel invasions by opportunistic species such as Bermuda grass, ultimately reducing tourism and having negative economic impacts. Furthermore, there is strong evidence that accumulation of *Sargassum* in coastal waters has detrimental impacts on fish, invertebrates, seagrass beds, and coral reefs (Lapointe 1997, Van Tussenbroek et al. 2017, Rodríguez-Martínez et al. 2019, Chávez et al. 2020). It is also important to note the potential negative effects of current uses of *Sargassum*, such as fertilizer for livestock feed, which could have implications for human consumption. However, it remains unknown to us if the bioaccumulation and biomagnification arsenic in plants fertilized by *Sargassum* reach levels that are toxic for human consumption.

Our results challenge the notion that ecosystems can't process novel subsidies effectively. Specifically, the decomposition rates of *Sargassum* seaweed were similar in both the forest and beach habitats, and naïve microbes appeared to play a more prominent role in the forest. Additionally, nutrients mobilized faster in the forest environment, which may be attributed to the leachates from *Sargassum* providing resources, such as nitrates and dissolved organic carbon, usable by generalist decomposers. This contradicts the Home Field Advantage hypothesis, which predicts that microbial use of subsidies should be faster in the experienced habitat (Vivanco and Austin 2008). The fact that the familiar system decomposed *Sargassum* at a similar rate to the naïve system suggests that the idea that familiar systems process subsidies better needs to be reconsidered.

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**Figure 1**

Percent decomposition of initial dry mass of large (gray bars) and small (white bars) mesh bags at Beach (left column) and the Forest (right column) in November 2022 (A) and March 2023 (B). Error bars represent mean ± SE. Note that no values are reported for large mesh bags at the beach in March 2022, the lack of a bar does not indicate zero decomposition.

**Figure 2**

Mean arthropod abundance in large (10 mm) mesh bags over sampling period (August and November 2022) in the Beach (left column, panels A, C) and the Forest (right column, panels B, D). Error bars represent mean ± SE.

**Figure 3**

Ammonium (A,B), Nitrate (C,D), and Dissolved Organic Carbon (E,F) content (mg) per kg of sediment over sampling periods (August and November 2022, March and August 2023) by site (Beach A,C,E and Forest B,D,F). Light gray bars represent Control treatments and dark gray bars represent *Sargassum* treatments. Error bars represent mean ± SE. Note that no samples were collected at the Beach site in August 2022.

**Figure 4**

Grams of CO2 per m2 over an hour in Control and *Sargassum* plots at the Beach (A) and Forest (B). Error bars represent mean ± SE.

**Figure 5**

Mean percent cover of plot interiors over sampling period (August and November 2022, March and August 2023) at the Beach (A) and Forest (B). Shapes represent grass (●) and other plants (▲) and colors represent Control plots (gray) and *Sargassum* plots (black).

Error bars represent mean ± SE. Lower panels show the effect sizes by sampling period associated with the panel above (i.e., panel C effect sizes associated with panel A, and panel D effect sizes are associated panel B). Effect sizes were calculated using Cohen’s d (*Sargassum* vs. Control) for grass and other plants.

**Figure 6**

Mean percent cover of plot perimeter over sampling period (August 2022 and August 2023) at the Beach (A) and Forest (B). Shapes represent grass (●) and other plants (▲) and colors represent Control plots (gray) and *Sargassum* plots (black). Error bars represent mean ± SE. Lower panels show the effect sizes by sampling period associated with the panel above (i.e., panel C effect sizes are associated with panel A, and panel D effect sizes are associated panel B). Effect sizes were calculated using Cohen’s d (*Sargassum* vs. Control) for grass (●) and other plants (▲).

**Figure 7**

Mean crawling arthropod abundance in pitfall traps over sampling period (August and November 2022, and March 2023) in the Beach (top row, panels A, B) and the Forest (middle row, panels C,D). Arthropod abundances are separated by Controls (left column, panels A, C) and *Sargassum* (right column, panels B, D). Effect size plots are associated with plots above (i.e., panel E effect sizes are associated with panels A and B, panel F effect sizes are associated with panels C and D). Effect sizes were calculated using Cohen’s d (*Sargassum* vs. Control). Shapes represent Amphipoda (●), Arachnida (▲), and Hymenoptera (■) and error bars represent mean ± SE.

**Figure 8**

Mean flying arthropod abundance in pitfall traps over sampling period (August and November 2022, and March 2023) in the Beach (top row, panels A, B) and the Forest (middle row, panels C,D). Arthropod abundances are separated by Controls (left column, panels A, C) and *Sargassum* (right column, panels B, D). Effect size plots are associated with plots above (i.e., panel E effect sizes are associated with panels A and B, panel F effect sizes are associated with panels C and D). Effect sizes were calculated using Cohen’s d (*Sargassum* vs. Control). Shapes represent Amphipoda (●), Diptera (▲), and Hymenoptera (■) and error bars represent mean ± SE.

**Supplementary Figure 1**

Sargasso pile volume loss over sampling periods (August and November 2022, March and August 2023) as a percent (%) of original volume calculated for sargasso treatments in August 2022. Individual dots represent replicates at the Beach (black) and the Forest (white).

**Supplementary Figure 2**

Percent cover of grass (top four panels) and other plants (bottom four panels) over sampling periods (August 2022, November 2022, and March 2023). Control treatments (light gray) and *Sargassum* addition treatments (dark gray) are shown at Distance 1 (closest to plot perimeter) and Distance 2 (furthest from plot perimeter). Error bars represent mean ± SE.

**Supplementary Figure 3**

Proportion of cover categories in plot interiors over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the Beach site. Columns designate treatment type (left is Control and right is *Sargassum*) and rows represent treatment block.

**Supplementary Figure 4**

Proportion of cover categories in plot interiors over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the Forest site. Columns designate treatment type (left is Control and right is *Sargassum*) and rows represent treatment block.

**Supplementary Figure 5**

Proportion of cover categories in plot perimeter over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the Beach site. Columns designate treatment type (left is Control and right is *Sargassum*) and rows represent treatment block.

**Supplementary Figure 6**

Proportion of cover categories in plot perimeter over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the Forest site. Columns designate treatment type (left is Control and right is *Sargassum*) and rows represent treatment block.

Figure 1

A graph of different sizes of trees

Description automatically generated with medium confidence

Figure 2

A white squares with black letters

Description automatically generated

Figure 3

**A graph of different types of minerals

Description automatically generated with medium confidence**

Figure 4

A comparison of a graph

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Figure 5

A graph of different types of data

Description automatically generated with medium confidence

Figure 6

A graph of different types of trees

Description automatically generated with medium confidence

Figure 7 A graph of different types of graph

Description automatically generated with medium confidence

Figure 8

A graph of different sizes and numbers

Description automatically generated with medium confidence

**Supplementary Figure 1**

A graph of a number of months

Description automatically generated

**Supplementary figure 2**

**A graph of different types of plants

Description automatically generated with medium confidence**

**Supplementary figure 3**

A chart of different colored squares

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**Supplementary figure 4**

A chart with different colored squares

Description automatically generated

**Supplementary figure 5**

A chart of different colored squares

Description automatically generated

**Supplementary figure 6**

A chart with different colored squares

Description automatically generated